Late Cenozoic Tegulinae (Gastropoda: Trochidae) from southern Peru

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ABSTRACT

Four new fossil tegulines (Gastropoda: Trochidae) are described from southern Peru [*Chlorostoma quipua* new species (late Miocene to late Pliocene), *Intistoma pirqua* new genus, new species (early Pliocene), *Cantallocostoma panistostum* new genus, new species (late Miocene to early Pliocene), *Tegula* (s.l.) *masiasi* new species (early to middle Miocene)], as are Pliocene and Pleistocene occurrences of the extant *Chlorostoma atrum* (Lesson, 1830), *C. luctuosum* (d'Orbigny, 1841), *Cantallocostoma quadricostatum* (Wood, 1828), *Agathistoma patagonicum* (d'Orbigny, 1835), *T.* (s.l.) *melaleucos* (Jonas, 1844), and *T.* (s.l.) *tridentata* (Potiez and Michaud, 1838). These data show that the Peruvian chlorostomine group is too ancient to be a Pliocene sister group to Caribbean-Atlantic agathistomines; indicate additional eastern Pacific groups of tegulines exist with roots reaching into the Miocene; and further demonstrate the success of *A. patagonicum* as a widespread and long-lived teguline in austral waters. A small radiation of Peruvian chlorostomines during the late Pliocene coincided with a molluscan mass extinction event in the Peruvian Faunal Province.

Additional Keywords: Mollusk, *Tegula*, *Chlorostoma*, *Agathistoma*, Miocene, Pliocene, Cenozoic, Pisco Basin, Taxonomy

INTRODUCTION

Seven extant teguline species (Gastropoda: Trochidae) inhabit the cool coastal waters of the Peruvian Faunal Province. They are, according to their traditional nomenclature, *Tegula atra* (Lesson, 1830), *T. luctuosa* (d'Orbigny, 1841), *T. euryomphala* (Jonas, 1844), *T. ignota* Ramírez-Böhme, 1976, *T. tridentata* (Potiez and Michaud, 1838), *T. quadricostata* (Wood, 1828), and *T. patagonica* (d'Orbigny, 1835) (Alamo and Valdivieso, 1997; Véliz and Vasquez, 2000). An eighth species, *Tegula melaleucos* (Jonas, 1844), a species from warmer waters of northern Peru, does appear rarely at southern Peruvian latitudes. This teguline fauna is as diverse as that of the warm-water Panamic Faunal Province (Keen, 1971; Alamo and Valdivieso, 1997), although with mostly different species, and is more speciose than the teguline fauna of the Magellanic Faunal Province (four species), which is a subset of the Peruvian fauna (Forcelli, 2000).

The geological record of tegulines from the Peruvian Faunal Province is meager. *Tegula luctuosa*, *T. atra*, and *T. tridentata* are listed in Herm's (1969) study of Pliocene and Pleistocene mollusks from Chile. *Tegula luctuosa* and *T. melaleucos* were reported from upper Pliocene and Pleistocene beds of northern Peru (DeVries, 1986). Four new species of tegulines, considered to have early to middle Miocene age (DeVries and Frassinetti, 2003; Finger et al., 2007), have been described from the Navidad Formation of central Chile by Nielsen et al. (2004).

This paper documents four new fossil species and several previously known Recent species of tegulines in Neogene deposits of southern Peru, including the oldest known teguline from Peru, the early Miocene *Tegula* (s.l.) *masiasi* new species; creates two new genera of tegulines, *Cantallocostoma*, new genus, and *Intistoma*, new genus, each with a newly described Neogene fossil species in the Peruvian Faunal Province, *Cantallocostoma panistosum* new species and *Intistoma pirqua* new species, and each having a modern representative in the eastern Pacific Ocean, the Peruvian *C. quadricostatum* and Californian *I. aureotinctum* (Forbes, 1852); adopts a full generic status for *Tegula* (*Chlorostoma*); and provides evidence for a late Miocene origin of a western South American group of *Chlorostoma* species.

GEOLOGY

The late Cenozoic marine stratigraphy of southern Peruvian forearc basins has been described by Dunbar et al. (1990) and DeVries (1998). Teguline-bearing deposits crop out west of Nazca and throughout the Sacaco Basin (Fig. 1). These bioclastic conglomerates and sandstones, which were assigned to the La Planchada and Pisco for-

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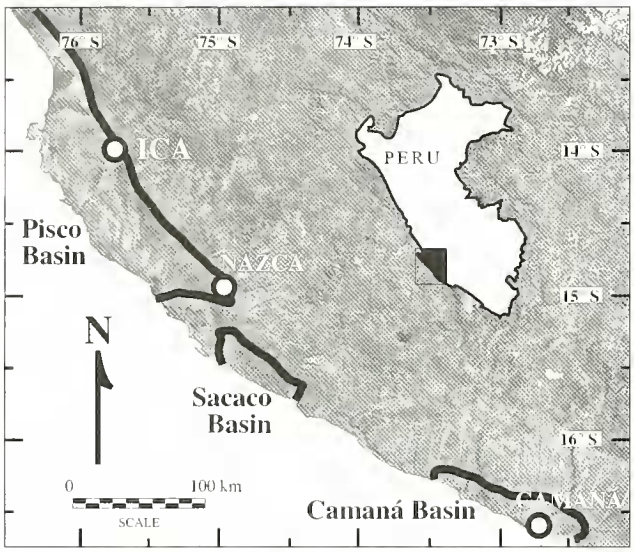


Figure 1. Location of onshore portions of Cenozoic forearc basins in southern Peru. New fossil species of *Tegula* are from Cenozoic deposits west and south of Nazca.

mations by Beaudet et al., 1976, and Muizon and DeVries, 1985, respectively, represent high-energy foreshore and intertidal environments lying close to mountainous paleo-shorelines and quieter foreshore and inner shelf environments lying hundreds to thousands of meters from paleo-shorelines defined by the beginning of the Andean foothills.

MATERIALS AND METHODS

Most Peruvian specimens described in this study were found by the author. Comparative material was studied at the Natural History Museum of Los Angeles County, Los Angeles, California, USA (LACM). Locality and sample descriptions are listed in the appendix. Lengths (L) and widths (W) are measured in millimeters, with dimensions of broken specimens enclosed by parentheses. A non-standard orientation for photographs of some specimens has been necessary to reveal important characters. Some figured specimens were coated with ammonium chloride. Types and numbered specimens, including those figured, are deposited at the Orton Geological Museum, Ohio State University, Columbus, Ohio USA (OSU); the Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM INV); and the Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington (UWBM). The prefixes "DV" refers to DeVries localities, "JM" to localities of J. Macharé (Instituto Geológico Minero y Metalúrgico, Lima, Peru), and "WJZ" to localities of W. J. Zinsmeister (Purdue University, Indiana, USA).

SYSTEMATICS

Superfamily Trochoidea Rafinesque, 1815
Family Trochidae Rafinesque, 1815
Subfamily Tegulinae Kuroda, Habe and Oyama, 1971
Genus *Tegula* Lesson, 1835

Type Species: *Trochus elegans* Lesson, 1835 (by monotypy) (= *Trochus pellisserpentis* Wood, 1828). Recent, Pacific coast of Central America.

Remarks: Resolving the difficult subfamilial placement of Tegulinae within Trochoidea (Hickman and McLean, 1990; Bouchet and Rocroi, 2005) is beyond the scope of this paper. *Tegula* itself has been assigned to three different subfamilies over the past century, but most taxonomists now refer it to the undiagnosed Tegulinae Kuroda, Habe, and Oyama, 1971 (Hickman and McLean, 1990). Only one extant teguline species, *Tegula pellisserpentis* (Wood, 1828), pertains to *Tegula* (s.s.) (Keen, 1971). Its combination of features (densely packed and heavily beaded spiral cords, tightly twisted columella, and numerous teeth extending from the columella across the apertural floor) is not seen in other species assigned to *Tegula*, so *T. pellisserpentis* is herein considered to be the monotypic representative of *Tegula* (s.s.), an opinion shared by J. H. McLean (pers. comm., 2006). Taxa often considered as subgenera of *Tegula*, e.g., *Chlorostoma* and *Agathistoma*, are elevated to generic status in this paper in accord with the practice of some authors (e.g., Arnold, 1907; Higo et al., 1999) and the opinion of J. H. McLean (pers. comm., 2006).

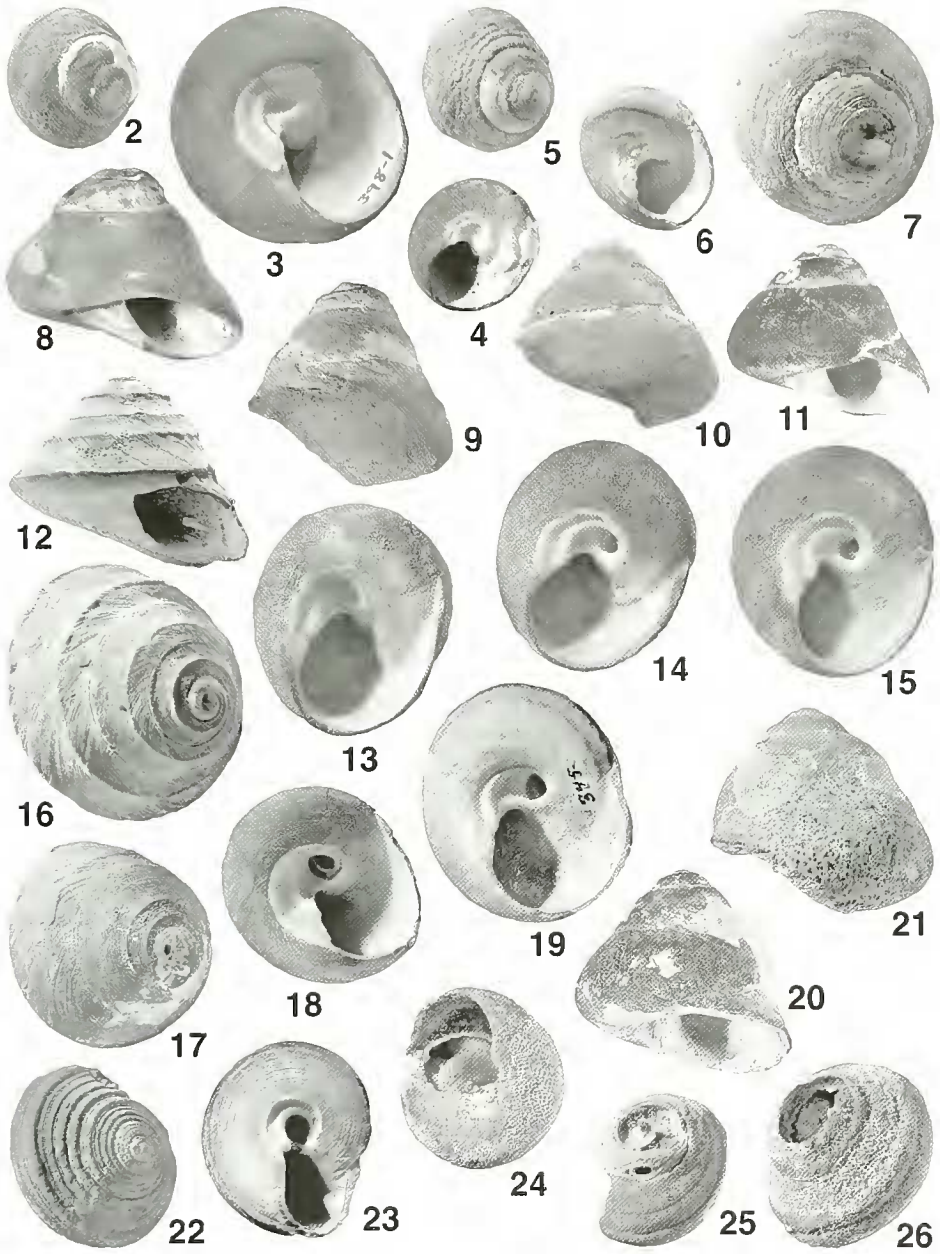
Genus *Chlorostoma* Swainson, 1840

Type Species: *Trochus argyrostomus* Gmelin, 1791 (by subsequent designation, Herrmannsen, 1846). Recent, Japan.

Remarks: Swainson (1840) erected *Chlorostoma* as a subgenus of *Trochus* Linnaeus, 1758, to include species with a "remarkably oblique" aperture, a very deep umbilicus, and one or two teeth on the outer (= lower part of inner?) lip. He assigned two species to *Chlorostoma*: *Trochus* (*Chlorostoma*) *argyrostoma* (= *Tegula argyrostoma* of authors) and *Trochus* (*Chlorostoma*) *umbilicaris* [= *Gibbula umbilicaris* (Linnaeus, 1758)]. Herrmannsen (1846) implicitly limited the definition of *Chlorostoma* by choosing *T. argyrostoma* as the type species. Examination of LACM material from the western North Pacific Ocean [*C. argyrostoma*, *C. lischkei* (Tapparone-Canefri, 1874), *C. rusticum* (Gmelin, 1791), *C. turbinatum* (A. Adams, 1853), *C. xanthostigma* (A. Adams, 1853)] shows that adult chlorostomine umbilici can be either open or closed. In the view of Grant and Gale (1931), *Chlorostoma* should be further restricted to toothed species having ventricose whorls, a nacreous interior, and a dark purplish exterior. This diagnosis makes possible the identification of Recent chlorostomine taxa from both sides of the North Pacific Ocean and in the eastern South Pacific Ocean.

Chlorostoma atrum (Lesson, 1830)
(Figures 2–4, 7–9, 13)

Trochus ater Lesson, 1830, vol. 2, pt. 1, p. 344, Mollusques, pl. 16, fig. 2; d'Orbigny, 1840: 409; Philippi, 1844, Abbildun-



Figures 2–4, 7–9, 13. *Chlorostoma atrum* (Lesson, 1830). **2.** UWBM 97863, DV 1372-1, Recent, oblique spire view, width = 9.8 mm. **3.** UWBM 97855, DV 398-1, Recent, basal view, width = 30.7 mm. **4.** UWBM 97863, oblique basal view. **7.** MUSM INV 126, DV 1252-1, early Pleistocene, oblique spire view, width = 27.1 mm. **8.** UWBM 97855, apertural view. **9.** UWBM 97860, Paracas Hotel, Recent, lateral view, length = 22.2 mm. **13.** UWBM 97860, oblique basal view, width = 23.4 mm. **Figures 5, 6.** *Chlorostoma funebralis* (A. Adams, 1855). UWBM 97862, south of La Jolla, California, Recent, width = 13.4 mm. **5.** Oblique spire view. **6.** Oblique basal view. **Figures 10–12, 14–19.** *Chlorostoma luctuosum* (d'Orbigny, 1841). **10.** UWBM 97864, Paracas Hotel, Recent, lateral view, length = 20.2 mm. **11.** UWBM 97865, Paracas Hotel, Recent, apertural view, length = 20.5 mm. **12.** UWBM 97866, Hueco La Zorra, Peru, Recent, apertural view, length = 21.6 mm. **14.** UWBM 97864, oblique basal view, width = 23.7 mm. **15.** UWBM 97865, basal view, width = 24.4 mm. Figure 16. UWBM 97866, oblique spire view, width = 28.5 mm. **17.** UWBM 97867, Lomas, Peru, Recent, oblique spire view, width = 26.4 mm. **18.** UWBM 97867, oblique basal view. **19.** UWBM 97868, Chile, Pleistocene, oblique basal view, width = 37.3 mm. **Figures 20, 21.** *Chlorostoma curyomphalum* (Jonas, 1844). UWBM 97871, DV 1599-1, Recent, length = 26.0 mm. **20.** Apertural view. **21.** Lateral view. **Figures 22, 23.** *Chlorostoma ignotum* (Ramírez-Böhme, 1976). UWBM 97872, Pellehue, Chile, Recent, width = 17.5 mm. **22.** Oblique spire view. **23.** Basal view. **Figures 24–26.** *Chlorostoma quipua* new species. **24.** UWBM 97873, DV 1254-Bal 6, late early Pliocene, basal view, width = 17.3 mm. Note faint protractive stripes on base. **25.** MUSM INV 136, DV 571-1, syntype, late Miocene, oblique spire view, width = 17.0 mm. **26.** UWBM 97873, oblique spire view.

gen und beschreibungen neuer oder wenig gekannter Conchylien, v. 1, p. 188, pl. 5, fig. 6; Philippi, 1846, Die Kreiselschnecken oder Trochoideen, p. 198, pl. 30, fig. 1; Hupé, 1854, p. 142, Malacologia, pl. 4, fig. 2.

Monodonta atra Lesson.—Potiez and Michaud, 1838: 319, pl. 29, figs. 14, 15.

Tegula atra Lesson.—Dall, 1909: 239, pl. 24, fig. 4; Carcelles and Williamson, 1951: 262; Aldea and Valdovinos, 2005: fig. 8B.

Chlorostoma ater Lesson.—Mörch, 1850: 20.

Tegula (Chlorostoma) atra (Lesson, 1830).—Marincovich, 1973: 24, fig. 42; Alamo and Valdivieso, 1997: 13, fig. 25; Guzmán et al., 1998: 35, fig. 22; Forcelli, 2000: 61, fig. 87; Véliz and Vasquez, 2000: 759, fig. 1B.

Trochus moestus Jonas, 1844: 113; Philippi, 1846, Abbildungen und beschreibungen neuer oder wenig gekannter Conchylien, v. 2, pl. 6, fig. 5; Philippi, 1846, Die Kreiselschnecken oder Trochoideen, p. 199, pl. 30, fig. 2; Hupé, 1854: 147, Malacologia, pl. 4, figs. 3, 3a, 3b.

Tegula moesta (Hupé, 1854).—Dall, 1909: 239; Alamo and Valdivieso, 1997: 14.

Chlorostoma minor Mörch, 1850: 20.

Diagnosis: Shell width about 40 mm; last whorl broadly rounded, including shoulder; keels lacking. Umbilicus of juvenile and adult shells white, closed; umbilicus with two well exposed spiral cords, the adaxial cord terminating in a columellar tooth.

Material Examined: UWBM 97855, DV 398-1, Recent, L = 25.0, W = 30.7; UWBM 97856, DV 398-1, lot of 2; UWBM 97857, DV 1252-1, L = 11.8, W = 18.6; UWBM 97858, DV 1418-1, latest Pliocene, L = (22.2), W = 30.2; UWBM 97859, DV 463-1, late Pleistocene, lot of 2; UWBM 97860, Paracas Hotel, Recent, L = 22.2; W = 23.4; UWBM 97861, Ipun, Chile, Recent, lot of 2; UWBM 97863, DV 1372-1, Recent, L = 8.0, W = 9.8; MUSM INV 126, DV 1252-1, early Pleistocene, L = (19.2), W = 27.1; MUSM INV 127, DV 1418-1, L = 31.4, W = 36.6; MUSM INV 128, DV 463-1, lot of 2.

Occurrence: Late Pliocene to middle Pleistocene: southern Peru to southern Chile. Late Pleistocene: southern Peru, Chile, southern Argentina. Recent: northern Peru to southern Chile, southern Argentina (G. Pastorino, pers. comm., 2002).

Remarks: Specimens of *Chlorostoma atrum* can exceed 40 mm in width and are generally smooth-shelled and purple-black, either entirely or dorsally, only. The last whorl is always broadly rounded; it lacks the keeled spiral cords present on specimens of *C. luctuosum*. The base on some specimens of *C. atrum* has weak spiral threads; the spire of some also has one or more narrow spiral grooves that produce as many as 15 intervening low broad spiral cords (Figure 7), not unlike the spiral sculpture of the Californian *C. funebralis* (A. Adams, 1855) (Figures 5, 6).

The adult shell of *Chlorostoma atrum* is usually distinguished from that of other Peruvian chlorostomines by its closed umbilicus. [G. Collado (pers. comm., 2005) notes that juveniles of *C. luctuosum* and adults of the small *Tegula* (s.l.) *tridentata* occasionally have closed umbilici.] The white umbilical area on specimens of *C. atrum* has two spiral cords. A white inner cord rises from beneath the umbilical callus and terminates on the edge of the columella as a thickened tooth. A weakly developed white outer cord traces the boundary of the umbilical area and becomes flattened on the columella, not quite protruding far enough to produce a tooth. Rarely, one or two weak spiral spurs develop between the two umbilical cords in a nacreous area that lies adaperturally of a thin, glossy, umbilical veneer. They, too, do not extend far enough to produce columellar teeth.

Chlorostoma luctuosum (d'Orbigny, 1841)
(Figures 10–12, 14–19)

Trochus luctuosus d'Orbigny, 1841, v. 5, p. 409, pl. 76, figs. 16–19; Philippi, 1846, Die Kreiselschnecken oder Trochoideen, p. 153, pl. 25, figs. 4, 5; Hupé, 1854: 143.

Tegula luctuosa Orbigny.—Dall, 1909: 239; DeVries, 1986: 512, pl. 27, figs. 3, 4; Guzmán et al., 1998: 36, fig. 23; Véliz and Vasquez, 2000: 762, fig. 1D; Alamo and Valdivieso, 2000: 14; Aldea and Valdovinos, 2005: fig. 8E.

Diagnosis: Shell width to 35 mm. Last whorl with one to three spiral cords or keels. Adult umbilicus open; juvenile umbilicus usually open; umbilicus with two well exposed umbilical spiral cords, the adaxial cord terminating in a columellar tooth.

Material Examined: OSU 37596, DV 240-23, latest Pliocene, L = 19.5, W = 23.9; UWBM 97864, Paracas Hotel, Recent, L = 20.3, W = 23.7; UWBM 97865, Paracas Hotel, Recent, L = 20.5, W = 24.4; UWBM 97866, Hueco La Zorra, Recent, L = 21.6, W = 28.5; UWBM 97867, Lomas dump, Recent, L = (20.6), W = 26.4; UWBM 97868, WJZ 345, Chile, Pleistocene, L = 26.8, W = 37.3; UWBM 97869, DV 382-1, Pleistocene, L = (20), W = 28.4; UWBM 97870, WJZ 345, L = (35.0), W = 43.1; MUSM INV 129, DV 382-1, L = 20.6, W = 31.1; MUSM INV 130, JM 8220, Pleistocene, lot of 2.

Occurrence: Late Pliocene to upper Pleistocene: northern Peru to Tongoy, central Chile. Recent: Galapagos Islands to Concepción, central Chile (southern limit from LACM collections).

Remarks: Specimens of *Chlorostoma luctuosum* are large and purple-black, either entirely or dorsally, only. Adult specimens are generally distinguished from specimens of *C. atrum* by having an open umbilicus and from both *C. atrum* and *C. euryomphalum* by having one to three primary spiral cords or keels: one near the base of the whorl, forming the periphery (Figure 12); another about one quarter of the distance anteriorly from suture to suture (Figure 12); and a third occasionally developed just anterior to the periphery (Figure 19). Some specimens of *C. luctuosum* are also covered with tertiary spiral threads (Figures 17, 18). The thin umbilical veneer and columellar teeth are identical to those on specimens of *C. atrum*, as are the umbilical cords, except that they are exposed coiling deep into the umbilicus.

Chlorostoma euryomphalum (Jonas, 1844)
(Figures 20, 21)

Trochus euryomphalus Jonas, 1844: 113; Philippi, 1844, Abbildungen und beschreibungen neuer oder wenig gekannter

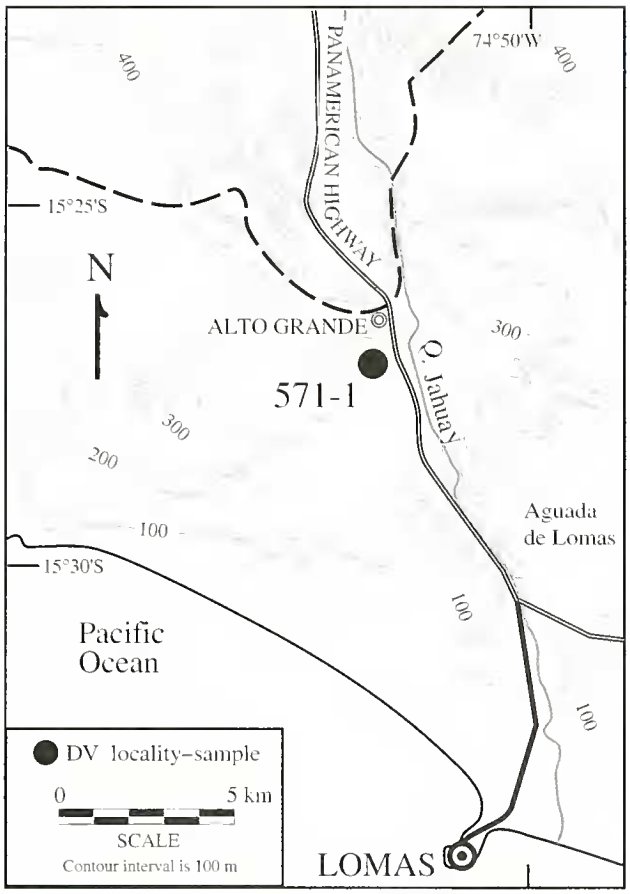


Figure 41. Type locality (DV 571-1) of *Chlorostoma quipua* new species.

Conchylien, v. 2, p. 27, pl. 6, fig. 4; Philippi, 1846, Die Kreiselschnecken oder Trochoideen, p. 155, pl. 25, fig. 7.

Tegula euryomphala (Jonas, 1844).—Carcelles and Williamson, 1951: 262.

Tegula euryomphalus [*sic*] (Jonas).—Dall, 1909: 239; Alamo and Valdivieso, 1997: 14.

Tegula euryomphala (Jones, 1844) [*sic*].—Guzmán et al., 1998: 36, fig. 25; Véliz and Vasquez, 2000: 762, fig. 1E; Aldea and Valdovinos, 2005: fig. 8C.

Trochus kieneri Hupé, 1854, p. 144, Malacologia, pl. 4, figs. 1, 1a, 1b.

Diagnosis: Shell width to 35 mm. Last whorl broadly rounded. Umbilicus white, open; umbilicus with two well exposed spiral cords, the adaxial cord terminating in a columellar tooth.

Material Examined: UWBM 97871, DV 1599-1, Recent, L = 26.0, W = 29.9.

Occurrence: Late Pleistocene: Northern to central Chile. Recent: Southern Peru to central Chile.

Remarks: Specimens of *Chlorostoma euryomphalum* are large, purple-black, and characterized by a broad open umbilicus and broadly rounded whorls. They differ from specimens of *C. atrum*, which have a closed umbilicus, and *C. luctuosum*, which have one or more angular spiral cords or keels. On some specimens of *C. luctuosum*, however, including Recent Peruvian and Chilean examples from LACM collections, Pleistocene Chilean specimens from WJZ collections, and upper Pliocene Peruvian specimens from northern Peru, the spiral cords are so weak that assigning the material to *C. luctuosum* or *C. euryomphalum* is problematic.

Chlorostoma ignotum (Ramírez-Böhme, 1976)
(Figures 22, 23)

Tegula ignota Ramírez-Böhme, 1976: 3, figs. 1–6; Forcelli, 2000: 61, fig. 8S; Véliz and Vasquez, 2000: 762, fig. 1F; Aldea and Valdovinos, 2005: fig. 8D; Collado and Brown, 2005: 131.

Diagnosis: Shell width to 30 mm. Outer layer slate colored. Sculpture consists of several well developed, unbeaded, primary spiral cords. Umbilicus open.

Material Examined: UWBM 97872, La Rinconada, Pellubue, Chile, Recent, L = 11.1, W = 17.5; UWBM 97906, Ipun, Chile, Recent, L = 29.4, W = 32.6.

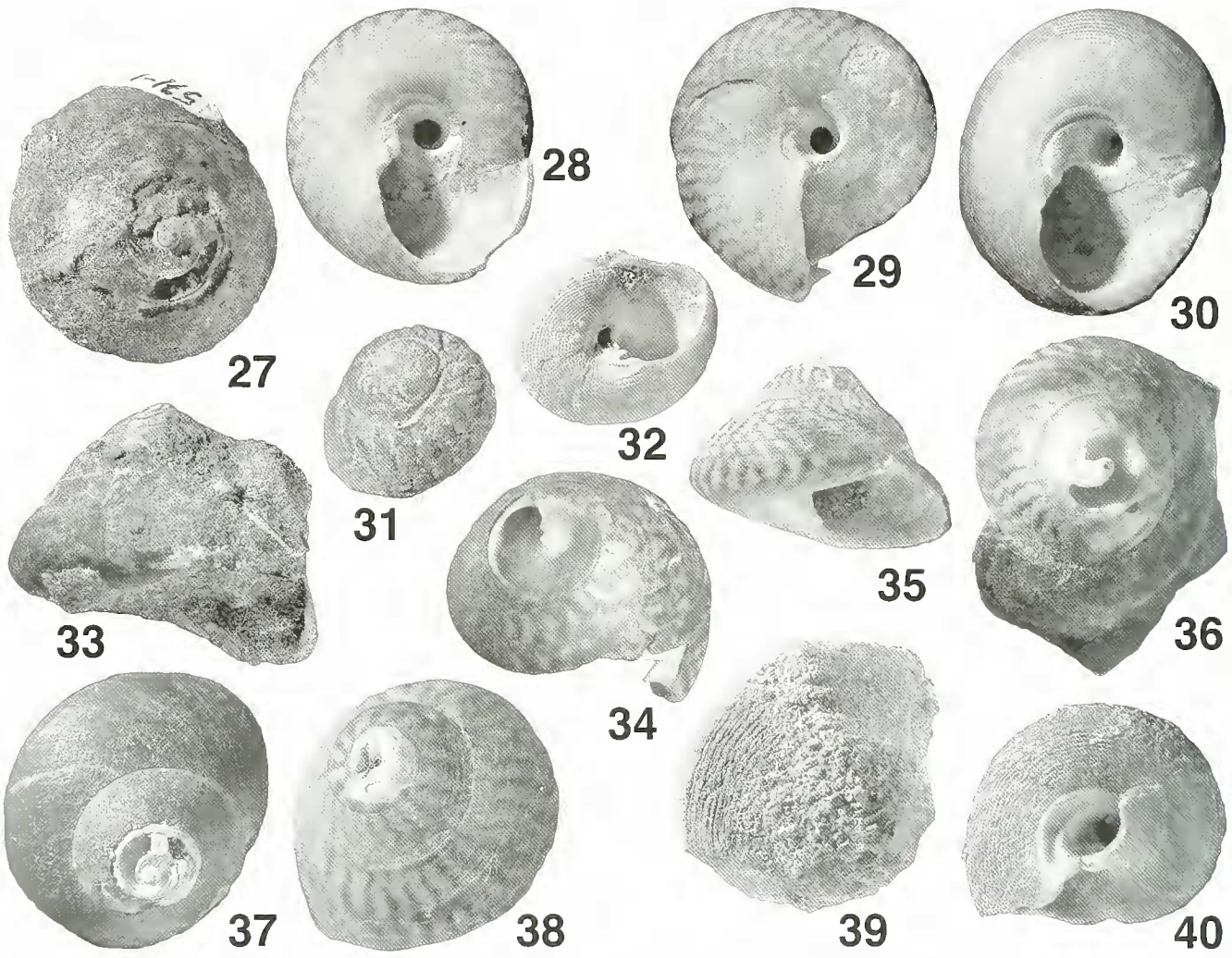
Occurrence: Recent: central to southern Chile.

Remarks: *Chlorostoma ignotum* is known only as a Recent species from Chile (e.g., Collado and Brown, 2005). Specimens of *C. ignotum* differ from those of other extant chlorostomines of the Peruvian Faunal Province in two significant respects: they lack the purple-black outer shell layer of *C. atrum*, *C. luctuosum*, and *C. euryomphalum*, being rather slate colored, and they have numerous, prominent, well-differentiated primary and secondary spiral cords between the periphery and suture and to a lesser extent on the base. The well-exposed umbilical cords, thin umbilical veneer, and columellar teeth are identical, however, with those of other species of South American *Chlorostoma*, and the strong spiral cords (Figure 22) are like those seen on rare specimens of early Pliocene *C. quipua* new species (Figures 25, 26; see below).

Chlorostoma quipua new species
(Figures 24–40)

Diagnosis: Adult whorls purple-black dorsally; spire and base usually light brown, commonly with dark brown protractive stripes or mottling. Umbilicus narrow, open.

Description: Shell up to 30 mm wide. Spire angle about 80 degrees. Periphery near base, sharply rounded to slightly angular. Sutures appressed. Protoconch unknown; teleoconch with five flat-sided to slightly convex whorls. Axial sculpture absent or rarely with rugose protractive ribs. Thin growth lines strongly prosocline. Spiral sculpture of 20 muted spiral threads posterior to periphery; rarely with three to five spiral grooves separating four to six broad low spiral cords or without spiral sculpture. Twenty to 30 evenly spaced spiral threads on base of juvenile specimens, muted or obsolete on adult whorls. Outer shell layer purple-black on adult whorls, tan or light brown on spire whorls and base. Protractive and rarely retrotractive wrinkled brown stripes usually



Figures 27–40. *Chlorostoma quipua* new species. **27.** MUSM INV 131, DV 571-1, syntype, spire view, width = 28.4 mm. **28.** MUSM INV 133, DV 1635-2, early Pliocene, basal view, width = 16.0 mm. **29.** UWBM 97880, DV 1635-2, basal view, width = 16.6 mm. **30.** UWBM 97879, DV 1635-2, basal view, width = 18.5 mm. **31.** UWBM 97890, DV 1598-1, early Pliocene, oblique spire, width = 11.2 mm. **32.** UWBM 97883, DV 1284-1, Pliocene, oblique basal view, width = 8.9 mm. **33.** UWBM 97876, DV 571-1, syntype, apertural view, length = 22.7 mm. **34.** UWBM 97880, oblique spire view. **35.** MUSM INV 133, apertural view. **36.** UWBM 97881, DV 1029-1, early Pliocene, spire view, width = 17.4 mm. **37.** UWBM 97879, oblique spire view. **38.** MUSM INV 135, DV 1029-1, oblique spire view, width = 11.3 mm. **39.** UWBM 97878, DV 809-1, Pliocene, spire view, width = 22.1 mm. **40.** MUSM INV 132,DV 809-1, basal view, width = 19.0 mm.

present on base and less often on spire. Inside edge of outer lip smooth. Umbilicus open, narrow; umbilical veneer thin. Columella with thick inner tooth at end of well-exposed white spiral umbilical cord. Weak outer tooth adjacent to floor of aperture at end of thin spiral cord following outer margin of umbilical area. Small parietal flange barely overhanging umbilicus.

Type Locality: DV 571-1, Alto Grande, about one km south of intersection with abandoned paved road to San Juan de Marcona, on south-facing hillside west of Panamerican Highway; one of several shell banks of the Pisco Formation (Figure 41). Locality inaccurately referred to as El Jahuay in Muizon and DeVries (1985). 15°26′37″S, 74°52′06″W (Acarí 1:100,000 quadrangle). Middle upper Miocene.

Type Material: (All DV 571-1, all syntypes) UWBM 97876, L = 22.7, W = 27.3; UWBM 97877, L = (17), W = (25.1); MUSM INV 131, L = (18.9), W = 28.4; MUSM INV 136, L = (10.2), W = 17.0.

Other Material Examined: UWBM 97873, DV1254-Bal 6, late early Pliocene, L = (11.0), W = 17.3; UWBM 97874, DV 1254-Bal 10, late Pliocene, L = (4.8), W = 10.4; UWBM 97875, DV 1254-Bal 10, L = (14.1), W = 24.4; UWBM 97878, DV 809-1, Pliocene, L = 15.4, W = 22.1; UWBM 97879, DV 1635-2, early Pliocene, L = 12.2, W = 18.5; UWBM 97880, DV 1635-2, L = (11.3), W = 16.6; UWBM 97881, DV 1029-1, early Pliocene, L = (12.3), W = (17.4); UWBM 97882, DV 1029-1, L = (12), W = 16.7; UWBM 97883, DV 1284-1, Pliocene, L = (5.2), W = 8.9; UWBM 97890, DV 1598-1, early

Pliocene, L = 8.4, W = 11.2; MUSM INV 132, DV 809-1, L = 16.8, W = (19.0); MUSM INV 133, DV 1635-2, L = 11.2, W = 16.0; MUSM INV 134, 1635-2, lot of 2; MUSM INV 135, DV 1029-1, L = 6.9, W = 11.3.

Occurrence: Middle late Miocene to early late Pliocene: southern Peru.

Etymology: "Quipua," Latinized version of "quipu," Inca counting device of braided and knotted strings, evoked by the wrinkled brown stripes on the base and spire of this species.

Remarks: Specimens of *Chlorostoma quipua* differ from those of *C. euryomphalum* and *C. luctuosum* by having a narrower umbilical area, smaller parietal flange, and protractive brown stripes. Specimens of *C. quipua* lack the keeled spiral cords of *C. luctuosum* and closed umbilicus of *C. atrum*. Some specimens of *C. quipua*, both Miocene and Pliocene, have broad spiral cords (Figure 25) like those seen on the juvenile whorls of some specimens of *C. atrum* (Figure 7). A single specimen from upper Pliocene beds above Playa Huaellaco (Figure 26) has spiral cords as pronounced as the raised spiral cords on specimens of the modern Chilean *C. ignotum* (Figure 22). Some lower Pliocene specimens near Yanca (Figure 31) have coarse protractive axial ribs like those on some Asian chlorostomines.

Specimens of *Chlorostoma quipua* superficially resemble those of *C. gallina* (Forbes, 1852), a Pliocene-to-Recent species from California and Baja California (Grant and Gale, 1931; McLean, 1978), and *C. rugosum* (A. Adams, 1853), a Recent species from the Gulf of California (Keen, 1971). Specimens of all three species have some degree of purple-black color and protractive stripes on the spire and/or base. Specimens of *C. gallina* and *C. rugosum*, however, are more ventricose laterally and basally and have weak to prominent protractive axial ribs and stripes posterior to the base. Specimens of *C. gallina* usually have a closed umbilicus.

Shells of *Chlorostoma quipua* are found in upper Miocene beach deposits near Alto Grande (DV 571-1; see Muizon and DeVries, 1985) with specimens of *Chorus frassinetti* DeVries, 1997, and *Acanthina obesa* DeVries, 2003 (DeVries, 1997, 2003). Lower Pliocene specimens of *C. quipua* occur together with specimens of the muricid gastropods, *Concholepas kieneri* Hupé, 1854; *Xanthochorus ochuroma* DeVries, 2005; and *Herminespina saskiae* DeVries and Vermeij, 1997; and the turbinid gastropod, *Prisogaster mcleani* DeVries, 2006 (DeVries, 2005, 2006; DeVries and Vermeij, 1997).

Genus *Cantallocostoma* new genus

Type species: *Trochus quadricostatus* Wood, 1828. Recent, Peru and Chile.

Diagnosis: White to brown outer shell layer. Three to five beaded primary spiral cords. Umbilicus open, broad. Two adaxially situated spiral umbilical cords terminating in columellar teeth. Parietal wall vertical, without parietal flange overhanging umbilicus.

Description: Shell up to 35 mm in diameter. Whorls ventricose to quadrate; periphery weakly bicarinate. Spiral sculpture of three to five primary spiral cords broken into beads; interspaces with two to five continuous or weakly beaded tertiary threads. Base with four to five beaded or non-beaded primary spiral cords and intervening secondary cords and tertiary threads. Umbilical area white, tabulate, sharply defined, with margin of umbilical area flaring towards aperture as steeply inclined wall. Umbilicus open, broad, with two spiral umbilical cords situated adaxially, the innermost thicker; each cord terminating in columellar tooth. Third tooth sometimes present at base of columella. Umbilical veneer variably developed. Columella thin, upright, without parietal flange overhanging umbilicus. Floor of aperture with ledge but without teeth. Inner lip sometimes with four to six closely spaced low teeth.

Occurrence: Late Miocene to Pleistocene: southern Peru. Recent: northern Peru to Chile.

Etymology: "Cantalloc," site near Nazca, Peru, where subterranean aqueducts are reached from ground level by pre-Incaic stonewall-lined spiral paths that resemble the spiral umbilical cords of this genus.

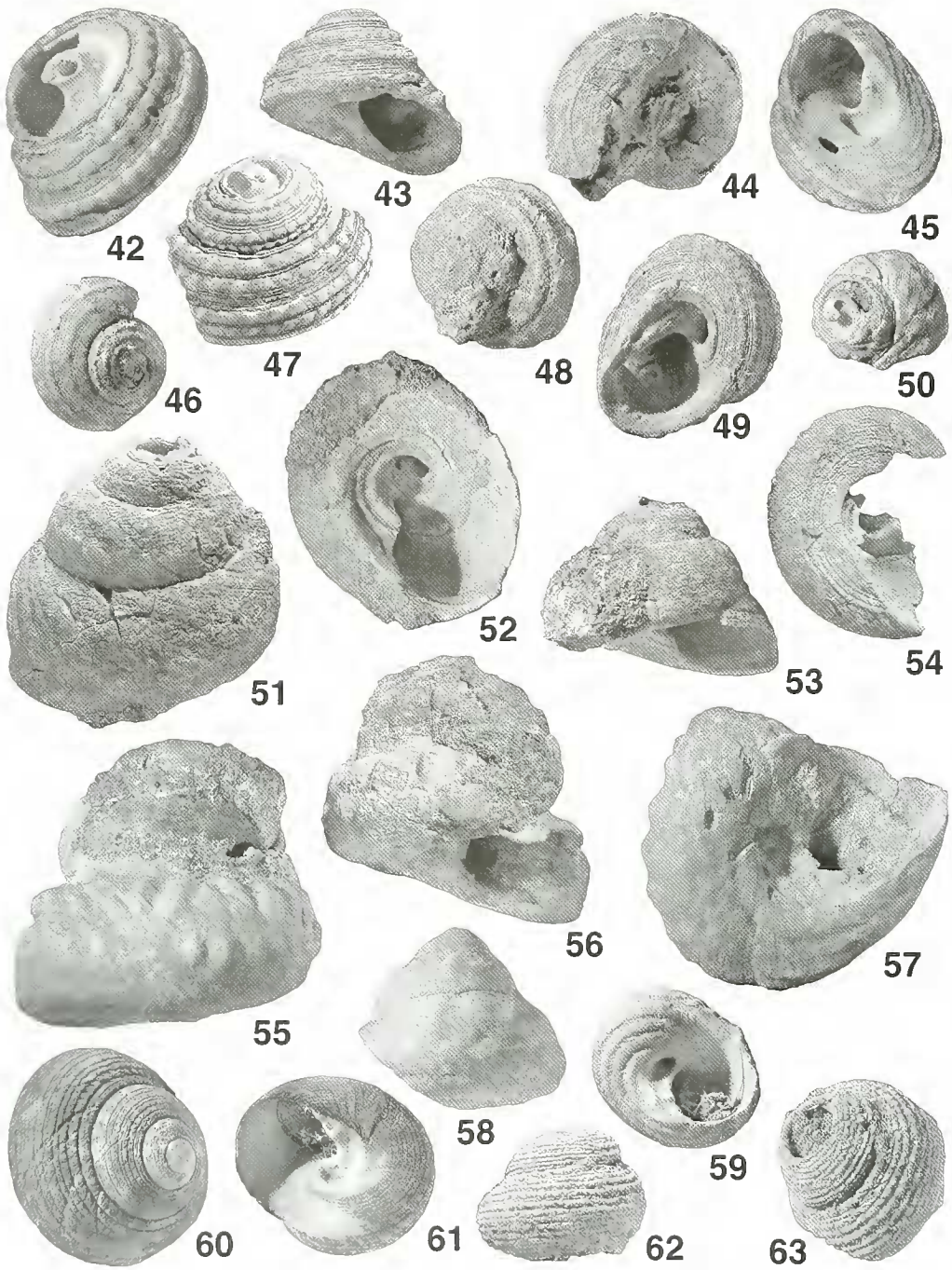
Remarks: Specimens of *Cantallocostoma* differ from those of Asian, Californian, and Peruvian *Chlorostoma* by having beaded spiral cords and two adaxially situated umbilical spiral cords. They differ from specimens of *Intistoma* new genus, by having closely spaced beads and lacking a subsutural band of well-developed protractive nodes. Specimens of *Cantallocostoma* differ from tegulines traditionally assigned to *Agathistoma* by lacking hallmarks of that genus: "narrow open umbilicus, a smooth or finely beaded spiral sculpture, and a variegated surface coloration" (Olsson and Harbison, 1953: 351).

Cantallocostoma quadricostatum (Wood, 1828)
(Figures 42–45, 47–49)

Trochus quadricostata Wood, 1828: 16, pl. 5, fig. 16.
Trochus quadricostatus Wood.—Philippi, 1846, Die Kreiselschnecken oder Trochoideen p. 154, pl. 25, fig. 6.
Tegula quadricostata (Wood, 1828).—Véliz and Vasquez, 2000: 759, fig. 1A; Aldea and Valdovinos, 2005: 8F.
Tegula quadricostata Gray.—Dall, 1909: 240; Alamo and Valdivieso, 1997: 14.
Monodonta catenifera Potiez and Michaud, 1838: 318, pl. 29, figs. 12–13.
Trochus torulosus Philippi, 1843, Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien, v. 1, pl. 2, fig. 12.

Diagnosis: Low spire, white to cream-colored with purple along edges of sculptural elements. Sculpture of three to five prominent primary beaded spiral cords.

Material Examined: UWBM 97884, DV 1372-1, Recent, L = (14.4), W = 23.9; UWBM 97885, DV 1372-1, L = (13.3), W = (20.8); UWBM 97886, DV 1713-1, early



Figures 42–45, 47–49. *Cantallocostoma quadricostatum* Wood, 1828. **42.** UWBM 97884, DV 1372-1, Recent, oblique spire view, width = 23.9 mm. **43.** UWBM 97886, DV 1713-1, early Pleistocene, apertural view, width = 21.5 mm. **44.** MUSM INV 137, DV 1355-1, late Pliocene, basal view, width = 16.0 mm. **45.** UWBM 97884, oblique basal view. **47.** UWBM 97885, DV 1372-1, oblique lateral view, width = 20.8 mm. **48.** UWBM 97887, DV 1355-1, oblique spire view, width = 18.1 mm. **49.** UWBM 97886, oblique basal view. **Figures 46, 50–54.** *Cantallocostoma panistostum* new species. **46.** MUSM INV 141, DV 1635-2, early Pliocene, oblique spire view, width = 14.3 mm. **50.** UWBM 97891, DV 571-1, late Miocene, oblique spire view, width = 14.9 mm. **51.** UWBM 97889, DV 1598-1, syntype, oblique lateral view, width = 33.7 mm. **52.** UWBM 97889, oblique basal view. **53.** UWBM 97889, apertural view. **54.** MUSM INV 139, DV 1598-1, syntype, basal view, width = 24.9 mm. **Figures 55–57.** *Intistoma piriqua* new species. UWBM 97892, DV 470-1, syntype, early Pliocene, length = 38.9 mm. **55.** Lateral view. **56.** Apertural view (lighting from upper right). **57.** Oblique basal view. **Figures 58, 59.** *Intistoma aurcotinctum* (Forbes, 1852). South of La Jolla, California, Recent. **58.** UWBM 97896, lateral view, length = 20.0 mm. **59.** UWBM 97897, oblique basal view, width = 17.8 mm. **Figures 60–63.** *Agathistoma patagonicum* (d'Orbigny, 1835). **60.** UWBM 97893, Argentina, Recent, oblique spire view, width = 15.4 mm. **61.** UWBM 97893, oblique basal view. **62.** UWBM 97895, DV 1032-2, late Pliocene, lateral view, width = 12.7 mm. **63.** UWBM 97895, oblique spire view.

Pleistocene, L = (14.5), W = 21.5; UWBM 97887, DV 1355-1, late Pliocene, L = 12.6, W = 18.1; UWBM 97888, DV 1355-1, L = (10.0), W = 16.1; MUSM INV 137, DV 1355-1, L = (8.9), W = 16.0; MUSM INV 138, DV 1355-1, L = 14.1, W = (19).

Occurrence: Late Pliocene: southern Peru. Recent: northern Peru to Chile.

Remarks: The number of primary beaded spiral cords on the last whorl of *Cantallocostoma quadricostatum* varies between three and five. Most modern specimens have two widely spaced primary spiral cords on the anterior half of the whorl and two closely spaced primary spiral cords adjacent to the posterior suture (Figure 42). Some specimens have an additional primary spiral cord between the two anterior spiral cords (Figure 47); other specimens have one of the two posteriormost primary spiral cords missing (Figure 43). The six known late Pliocene specimens from southern Peru (Figure 48) and single early Pleistocene specimen (Figure 43) have three primary spiral cords.

Cantallocostoma panistostum new species
(Figures 46, 50–54)

Diagnosis: Exterior uniformly pale brown; spiral sculpture of three beaded spiral cords. Basal spiral cords bunched towards umbilical area.

Description: Shell nearly 35 mm in diameter. Spire angle about 70 degrees. Periphery at base, sharply rounded. Sutures impressed. Protoconch unknown. Teleoconch with five quadrate whorls. Axial sculpture absent except for intermittently rugose prosocline growth lines. Spiral sculpture of closely beaded spiral cord at base and two posterior spiral rows of more widely spaced beads, about 25 per whorl, bracketing shoulder. Posterior beads sometimes slightly protractively elongate. Interspaces rarely with beaded secondary spiral cords; usually with wavering tertiary spiral threads. Base weakly convex, with six to ten closely spaced spiral cords adjacent to umbilical area. Outer shell layer pale brown, without color pattern. Inner edge of outer lip smooth. Umbilicus open, wide, with two adaxially situated spiral cords. Umbilical veneer thin. Innermost umbilical cord prominent, second cord thin; each terminates in columellar tooth. Third tooth at base of columella nearly obsolete. Columella thin; parietal flange absent.

Type Locality: DV 1598-1, roadcut along Panamerican Highway, shell beds exposed along descent from north into Río Yauca valley (Figure 64). 15°39′49″S, 74°31′50″W (Yauca 1:100,000 quadrangle). Lower Pliocene.

Type Material: (DV 1598-1, all syntypes) UWBM 97889, DV 1598-1, L = (25.2), W = 33.7; UWBM 97890, DV 1598-1, L = 8.4, W = 11.2; MUSM INV 139, DV 1598-1, L = (13.7), W = 24.9; MUSM INV 140, Panamerican roadcut at Yauca, early Pliocene, L = (17.9), W = 33.3.

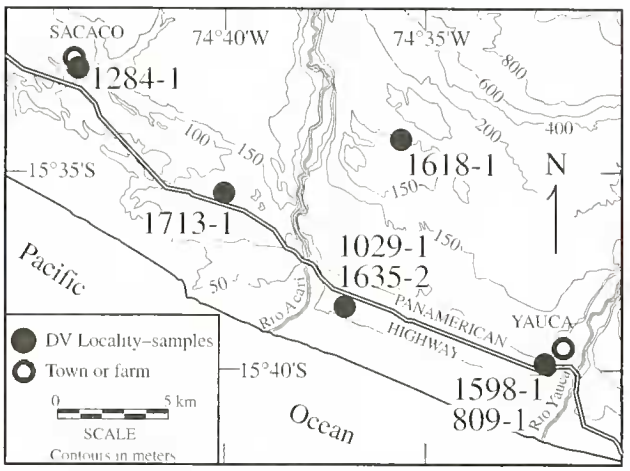


Figure 64. Type locality (DV 1598-1) of *Cantallocostoma panistostum* new species and other teguline localities between Sacaco and Yauca.

Other Material Examined: UWBM 97891, DV 571-1, late Miocene, L = 10.4, W = 14.9; MUSM INV 141, DV 1635-2, early Pliocene, L = 8.8, W = 14.3.

Occurrence: Late Miocene to early Pliocene: southern Peru.

Etymology: "Panis," Latin noun meaning "bread," and "tostum," Latin neuter past participle-adjective meaning "toasted," referring to the bread-crust color of this species.

Remarks: The light brown color of the outer shell layer on specimens of *Cantallocostoma panistostum* resembles that of specimens of *Tegula hemphilli* Oldroyd, 1921, a late Pliocene-to-Pleistocene species from California (Grant and Gale, 1931). Specimens of *T. hemphilli* and numerous other Miocene and Pliocene Californian teguline species with similar coloration lack the two umbilical spiral cords close to the axis and are covered by numerous closely spaced primary spiral cords, none of which are beaded.

Specimens of *Cantallocostoma panistostum* are found in upper Miocene nearshore sandstones with *Chlorostoma quipua*; *Chorus frassinetti* DeVries, 1997; *Acanthina obesa*; and *Xanthochorus stephanicus* DeVries, 2005; and in lower Pliocene cobbly bioclastic gravels associated with the mouth of the paleo-Río Yauca with disarticulated valves of an undescribed *Anadara* species, venerid bivalves, *Chlorostoma quipua*, *Xanthochorus ochuroma*, and *Concholepas nodosa* Möricke, 1896.

Genus *Intistoma* new genus

Type species: *Trochus aurcotinctus* Forbes, 1852. Pleistocene to Recent, California.

Diagnosis: Spiral sculpture of subsutural band of thick protractive nodes and peripheral and sub-peripheral primary spiral cords. Base with three thick, primary spiral cords. Umbilicus open.

Description: Shell up to 45 mm wide, spire angle about 75 degrees. Whorls four to five in number, quadrate to carinate; sutures weakly impressed. Protoconch unknown. Sculpture of thick rounded protractive axial ribs intersecting with an equally thick spiral cords, producing a broad subsutural spiral band of elongate protractive nodes, a near-basal peripheral band of stubby protractive nodes more numerous than nodes in the subsutural band, and a sub-peripheral primary spiral cord with little axial modification. Tertiary threads sometimes present; often corrugated by slightly raised strongly oblique lamellar growth lines. Umbilicus open. Columella thin; parietal flange erect to slightly overhanging umbilicus; parietal callus small. Umbilical veneer thick, covering all but wedge-shaped adapertural portion of umbilical wall. Umbilical spiral cord submerged in umbilical wall, emergent terminally as prominent columellar tooth. Smaller second columellar tooth sometimes present abaxially adjacent to first tooth.

Etymology: "Inti," the Inca sun god, with a nod to California's sunshine and the sunset-orange color inside the umbilicus of the type species, *Intistoma aureotinctum*.

Occurrence: Late Miocene or early Pliocene: southern Peru. Early Pleistocene to Recent: California.

Remarks: The new genus, *Intistoma*, is proposed for two very similar species: the Pleistocene-to-Recent Californian *Intistoma aureotinctum* and the early Pliocene Peruvian *I. pirqua* new species. Specimens of both species differ from those of nearly all other teguline taxa by possessing three thick primary spiral cords on the base, rather than cords that are more numerous and thinner. Specimens of *Intistoma* additionally differ from those properly assigned to *Agathistoma* by lacking teeth on the floor of the aperture and the inner edge of the outer lip and by lacking closely spaced beaded primary spiral cords.

Intistoma aureotinctum has been considered the extant representative of a lineage of Californian Neogene tegulines (Addicott, 1970) that includes the early Miocene *Tegula dalli arnoldi* Addicott, 1970, the late Miocene *Tegula nashae* Clark, 1915, and Pliocene *Tegula lemphilli* Oldroyd, 1921. Specimens of fossil Californian species do have a subsutural band of elongate protractive nodes, as do specimens of *Intistoma*, and some have thick peripheral spiral cords, but none have the distinctive intistomine combination of thick basal spiral cords and tertiary spiral threads across the entire surface of the whorls.

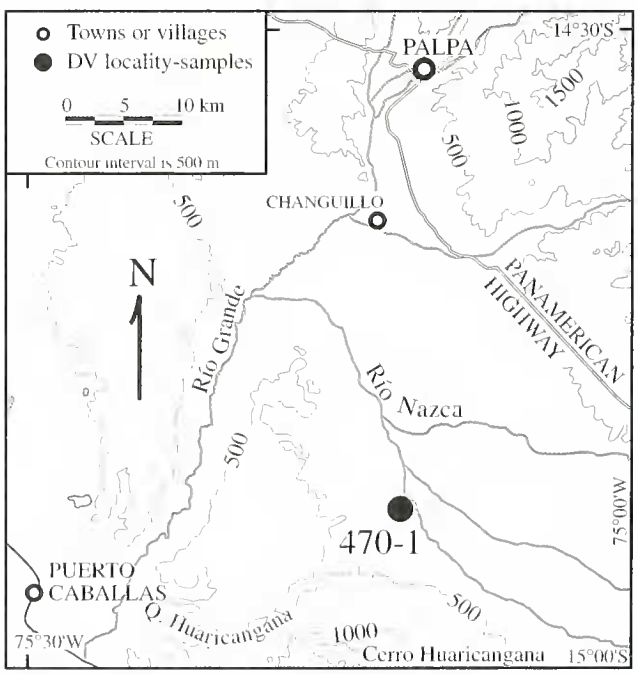
Intistoma pirqua new species
(Figures 55–57)

Diagnosis: Shell large, weakly bicarinate, with posterior row of protractive nodes. Base of shell with three broad spiral cords. Umbilicus open.

Description: Shell large, width more than 40 mm; spire angle about 60 degrees. Whorls ventricose, weakly bicarinate; sutures deeply impressed. Protoconch unknown; early spire whorls missing; teleoconch of at least three whorls. Last whorl with sculpture of about 18 elongate protractive ribs on posterior half of whorl; with about 21 circular to slightly protractively elongate nodes at periphery, two-thirds the distance from suture to base; and with a continuous low broad spiral cord at edge of base. Base with three low broad spiral cords, innermost cord bordering umbilical area and twice as wide as other two cords. Faint traces of secondary spiral cords in interspaces laterally and basally. Aperture oblique, outer lip and colabral growth lines moderately prosocline (40 degrees). Umbilicus open. Columella with at least one tooth, directed basally; anterior portion partly excavated, partly missing. Floor of aperture partly missing; no teeth evident.

Type Locality: DV 470-1, above rocky road from Hacienda Tinca to Quebrada Huaricangana; hillside of brown sandstone (Figure 65). 14°56′ S, 75°09′ W (Palpa 1:100,000 quadrangle). Upper Miocene or lower Pliocene.

Type Material: (DV 470-1, syntypes, late Miocene or



Figures 65. Type locality (DV 470-1) of *Intistoma pirqua* new species.

early Pliocene) UWBM 97892, L = (38.9), W = 43.4; MUSM INV 142, L = (32), W = (42).

Occurrence: Late Miocene to early Pliocene: southern Peru.

Etymology: "Pirqua," Latinized version of "pirqa," Quechua word for "wall," referring to the similarity of this species's sculpture and Incaic stone walls.

Remarks: The type specimens of *Intistoma pirqua* closely resembles specimens of *I. aureotinctum* (Figures 58, 59), differing principally by being twice the size in all dimensions and by having better developed nodes on the peripheral spiral cord. The specimens of *I. pirqua* were found together with specimens of *Chlamys simpsoni* (Philippi, 1887) and *Panopea coquimbensis* (d'Orbigny, 1842), both species from lower Pliocene beds in Chile (Herm, 1969) and southern Peru (Muizon and DeVries, 1985).

Genus *Agathistoma* Olsson and Harbison, 1953

Type Species: *Trochus viridulus* Gmelin, 1791 (by original designation). Recent, Caribbean and northeastern South America.

Remarks: One of two Recent specimens of *Agathistoma patagonicum* from Argentina (UWBM 97893) lacks an open umbilicus (Figure 61), as do some specimens of the Pliocene Sierra Laziar outcrops in Argentina (Ihering, 1907), suggesting either that the character is not diagnostic for all species of *Agathistoma* (Olsson and Harbison, 1953) or that the species in question might not be a member of the *Agathistoma* group.

Agathistoma patagonicum (d'Orbigny, 1835)
(Figures 60–63)

Trochus (*Monodonta*) *patagonicus* d'Orbigny, 1835, vol. 3(4), p. 155; d'Orbigny, 1840, vol. 5(3), p. 408, pl. 55, figs. 1–4.
Neomphalius patagonicus (Orb.). —Ihering, 1907: 400.
Tegula patagonica Orbigny.—Dall, 1909: 240; Alamo and Valdivieso, 1997: 14; Forcelli, 2000: 62, fig. 89.
Tegula (*Agathistoma*) *patagonica* (d'Orbigny, 1835).—Rios, 1985: 20, pl. 9, fig. 77; Del Río, 1998: 27, pl. 1, figs. 16–17.
Trochus corrugatus Philippi, 1844, Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien, v. 1, p. 67, pl. 2, fig. 7.
Trochus fuscesens Philippi, 1844, Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien, v. 1, p. 92, pl. 3, fig. 8.
Trochus orbignyana Pilsbry, 1900: 110; Carcelles, 1945: 38, pl. 1, figs. 6, 7, 12–15.

Material Examined: UWBM 97893, Cabo dos Bahías, Chubut Province, Argentina, Recent, L = 11.2, W = 15.4; UWBM 97894, Cabo dos Bahías, Chubut Province, Argentina, Recent, L = 11.6, W = 14.6; UWBM 97895, DV 1032-2, late Pliocene, L = (9), W = 12.7.

Diagnosis: Shell under 20 mm wide. Sculpture of closely spaced beaded primary spiral cords with intercalated secondary cords; beading sometimes obsolete. Columella with three teeth; umbilicus open or closed.

Occurrence: Late early to middle Miocene: Argentina (Ihering, 1907). Late Pliocene: southern Peru. Recent: northern Peru to Chile, southern Brazil to Argentina.

Remarks: A single incompletely preserved specimen of an agathistomine was found between Yanca and Chala in bioclastic deposits just below the highest marine terrace at 200 meters above sea level. Associated taxa that are either locally or entirely extinct [*Prisogaster valenciai* DeVries, 2006; *Acanthina triangularis* DeVries, 2003; *Chorus giganteus* (Lesson, 1830); *Concholepas camerata* DeVries, 2000; *Xanthochorus xuster* DeVries, 2005] are indicative of a late Pliocene age (DeVries, 1997; 2000; 2003; 2005; 2006).

The closely spaced beaded spiral cords on the southern Peruvian agathistomine resemble those on specimens of *Agathistoma verrucosum* McLean, 1970, and *A. pictum* McLean, 1970, Panamic species which presently range as far south as northern Peru (Alamo and Valdivieso, 1997), but the base of the Peruvian Pliocene specimen is not as flattened as it is on specimens of the northern Peruvian species and the spiral cords are more closely spaced, suggesting an assignment to *A. patagonicum*.

Genus or Subgenus indeterminate

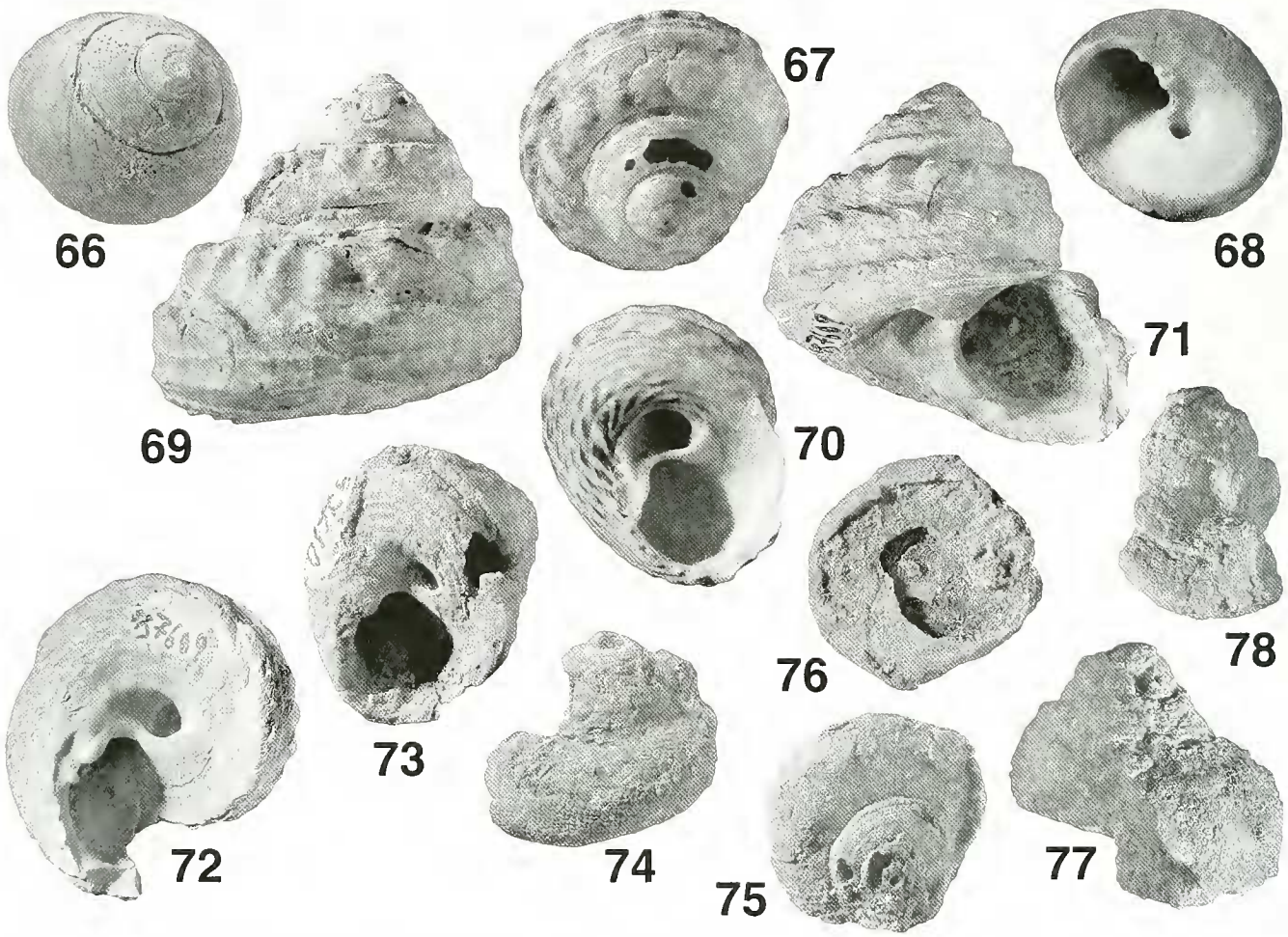
Tegula (s.l.) *tridentata* (Potiez and Michaud, 1838)
(Figures 66, 68)

Monodonta tridentata Potiez and Michaud, 1838, vol. 1, p. 321, pl. 29, figs. 16–17.
Trochus tridentatus Potiez and Michaud.—Philippi, 1846, Die Kreiselschnecken oder Trochoideen, p. 153, pl. 25, fig. 3.
Tegula tridentata (Potiez and Michaud).—Dall, 1909: 176; Carcelles and Williamson, 1951: 262; Herm, 1969: 91; Aldea and Valdovinos, 2005: fig. 8G.
Tegula (*Chlorostoma*) *tridentata* (Potiez and Michaud, 1838).—Marincovich, 1973: 24, fig. 43; Véliz and Vasquez, 2000: p. 761, fig. 1C; Guzmán et al., 1998: 36, fig. 24; Forcelli, 2000: 90, fig. 60.
Trochus tridens Hupé, 1854: 145.

Material Examined: UWBM 97898, DV 1372-1, Recent, L = 7.0, W = 9.9; UWBM 97899, DV 401-1, Recent, lot of 5; UWBM 97900, DV 381-5, middle Pleistocene, L = (11.7), W = 14.0.

Occurrence: Middle Pleistocene: southern Peru to central Chile. Recent: northern Peru to southern Chile.

Remarks: *Tegula tridentata* is a small, high-spired, purple-black species with an excavated white base. The exterior is usually smooth, but some specimens have low broad primary spiral cords on juvenile whorls. A narrow open umbilicus is bordered by a white columella with three teeth. The two teeth closest to the axis lie at the end of umbilical spiral cords, the outermost of which is mostly submerged beneath a thick umbilical veneer. The third tooth is situated adjacent to the floor of the aper-



Figures 66, 68. *Tegula* (s.l.) *tridentata* (Potiez and Michaud, 1838). UWBM 97898, DV 1372-1, Recent, width = 9.9 mm. **66.** Oblique spiral view. **68.** Oblique basal view. **Figures 67, 69–72.** *Tegula* (s.l.) *melaleucos* (Jonas, 1844). **67.** UWBM 97901, Paracas Hotel, Recent, oblique spire view, width = 23.9 mm. **69.** OSU 37609, DV 211-3, late Pleistocene, lateral view, length = 28.2 mm. **70.** UWBM 97901, oblique basal view. **71.** OSU 37609, apertural view. **72.** OSU 37609, oblique basal view, width = 29.0 mm. **Figure 73.** *Tegula* (s.l.) (?) *rubroflammulata* (Koch in Philippi, 1843). OSU 37610, DV 341, early Pleistocene, oblique basal view, width = 22.0 mm. **Figures 74–78.** *Tegula* (s.l.) *masiasi* new species. **74.** UWBM 97904, DV 478-1, early Miocene, lateral view, length = 16.6 mm. **75.** UWBM 97903, DV 1019-1, holotype, middle Miocene, oblique spire view, width = 15.9 mm. **76.** UWBM 97903, basal view. **77.** UWBM 97905, DV 1648-1, early Miocene, lateral view, length = 14 mm. **78.** UWBM 97905, basal view showing edge of umbilical area, width = 16.9 mm.

ture. The inside of the outer lip often has four to six short elongate teeth. In the latter three characters the species resembles *Cantallocostoma quadricostatum*, with which it has been grouped using mitochondrial DNA sequences by Hellberg (1998), who placed the species with *Agathistoma*. In its color and obsolete spiral sculpture, however, "*tridentata*" specimens greatly resemble Peruvian species of *Chlorostoma*, to which they were assigned by Marincovich (1973) and Guzmán et al. (1998). The only fossil example of *T. tridentata* in Peru comes from a middle Pleistocene marine terrace bed near San Juan de Marcona, southern Peru.

Tegula (s.l.) *melaleucos* (Jonas, 1844)
(Figures 67, 69–72)

Trochus melaleucos Jonas, 1844: 169; Philippi, 1846, Die Kreiselschnecken oder Trochoideen, p. 185, pl. 28, fig. 16.

Tegula melaleucos (Jonas). —Dall, 1909: 239.

Tegula (*Agathistoma*) *melaleucos* (Jonas, 1844).—Keen, 1971: 340, fig. 106; Alamo and Valdivieso, 1997: 13, fig. 22.

Not *Tegula* (*Agathistoma*) *melaleucos* (Jonas, 1844).—DeVries, 1986: 515, pl. 27, figs. 1, 2, 10, 12 [possibly *Tegula* (s.l.) *rubroflammulata* (Koch in Philippi, 1843)].

Material Examined: OSU 37609, DV 211-3, late Pleistocene, L = 28.2, W = 29.0; UWBM 97901, Paracas Hotel, Recent, L = 17.3, W = 23.9; UWBM 97902, northern Peru, Recent, L = (11.5), W = 20.1. Specimens assigned to *Tegula melaleucos* by DeVries (1986) but more likely belonging to *Tegula* (s.l.) *rubroflammulata*: OSU 37610, DV 341, early Pleistocene, L = 22.0, W = 22.0; OSU 37611, DV 341, L = (14.8), W = (18.0).

Occurrence: Recent: northern Peru; rarely in southern Peru.

Remarks: Specimens of *Tegula melaleucos* are characterized by a strongly bicarinate periphery, a line of protractive nodes between the periphery and suture, and protractive brown stripes laterally and basally, where they spiral into an open umbilicus. A single spiral cord emerges from the umbilicus and is truncated by a columellar ridge that ends in a basally projecting tooth. A second prominent tooth protrudes at the juncture of the columella with the floor of the aperture, and additional small teeth may occur along the edge of a beveled ledge that passes just inside the floor of the aperture.

Imperfectly preserved specimens of *Tegula* from the uppermost Pliocene / lower Pleistocene Mancora Tablazo of northern Peru (Figure 73; DeVries, 1986; 1988) have less impressed sutures and more convex profiles than typical specimens of *T. melaleucos* and nodes near the suture that are not protractive. These specimens are better referred to *T. rubroflammulata*, a Recent species that had been reported to range only as far south as Colombia (Keen, 1971).

Tegula (s.l.) *masiasi* new species
(Figures 74–78)

Diagnosis: Spire whorls with broad spiral cords; umbilicus narrow, open; shell lacking purple-black outer layer.

Deseription: Shell conical, up to 16 mm wide. Spire angle about 70 degrees. Periphery at base; angular. Sutures appressed to impressed. Protoconch unknown; teleoconch with at least four flat-sided to convex whorls. Axial sculpture absent; colabral growth lines strongly prosocline. Spiral sculpture absent or with several broad, low spiral cords on spire. Outer shell layer lacking purple-black color. Base flattened to weakly convex, without visible spiral sculpture. Inner side of outer lip smooth. Umbilicus open. Columella thin, with at least one tooth at end of umbilical cord. Parietal flange barely overhanging umbilicus.

Type Locality: DV 1019-1, Gramonal, about one-half km east of mouth of Quebrada Gramonal, on bluff overlooking road to Fundo Santa Rosa (Figure 79). 14°45′50″S, 75°30′22″W (Lomitas 1:100,000 quadrangle). Lower middle Miocene.

Type Material: UWBM 97903, DV 1019-1, holotype, early middle Miocene, L = (7), W = 15.9.

Other Material Examined: UWBM 97904, DV 478-1, early Miocene, L = 16.6, W = (21.8); UWBM 97905, DV 1648-1, early Miocene, L = 14.0, W = 16.9; MUSM INV 143, DV 1648-1, L = 14.6, W = 19.8

Occurrence: Early to early middle Miocene; southern Peru.

Etymology: Named in honor of Antonio Masias, petroleum geologist from Arequipa, Peru, who has provided advice on Peruvian matters since we both attended Oregon State University in 1977–1978.

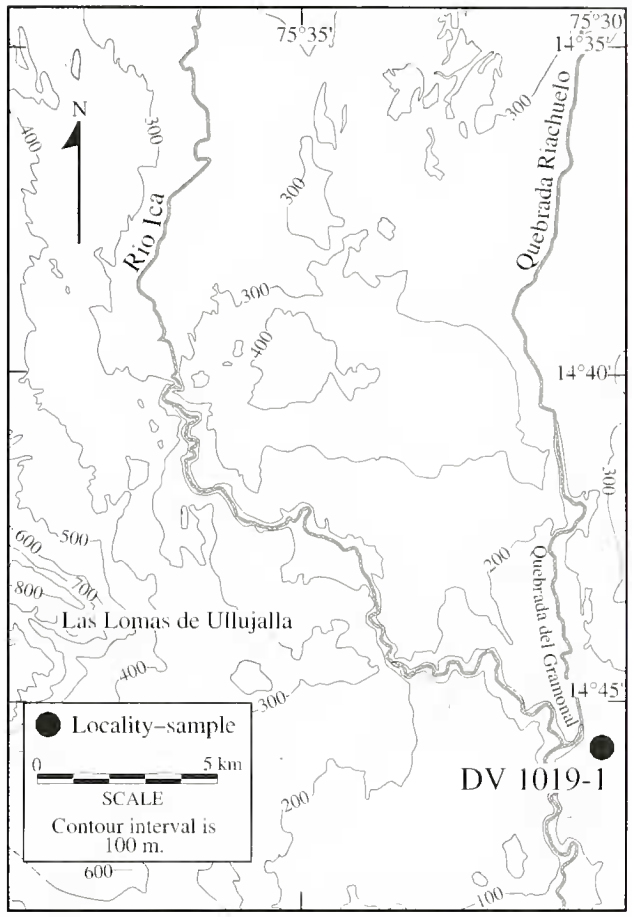


Figure 79. Type locality (DV 1019-1) of *Tegula* (s.l.) *masiasi* new species.

Remarks: Specimens of *Tegula* (s.l.) *masiasi* are the oldest known tegulines from the Pisco Basin; they occur near the base of a depositional sequence that unconformably underlies the Pisco Formation near Cerros Colorado (Figure 78), which implies the lower portion of the uppermost Oligocene to lower middle Miocene Chilcatay Formation (DeVries, 1998), as well as a few tens of meters above the base of the Pisco Formation, which indicates an early middle Miocene age (DeVries and Schrader, 1997). Despite the poor state of preservation, it does appear that these early and middle Miocene specimens are not chlorostomines, which first appear with their purple-black outer shell layer in beds at Alto Grande at about 9–10 Ma (Muizon and DeVries, 1985; DeVries and Schrader, 1997).

DISCUSSION

Fossils found since 1990 offer a new perspective on the origin of Tegulinae. Tegulines had been thought to have arisen during the early or middle Miocene (Hickman and McLean, 1990), based on knowledge of fossil taxa from Japan and California [e.g., *Tegula thea* Nomland, 1917,

and *T. varistriata* Nomland, 1917, Santa Margarita beds, California, upper Miocene (Nomland, 1917); *T. dalli* Arnold, 1907, and *T. dalli* var. *inornata* Arnold, 1907, Topanga Group, California, middle Miocene (Arnold, 1907; Yerkes and Campbell, 2005); *T. dalli arnoldi* Addicott, 1970, Olcese Sand, California, uppermost lower Miocene (Addicott, 1970; Sanchez and Prothero, 2003)]. The discovery of *T. jeanae* Squires and Saul, 2005, a late Campanian species from the Chico Formation of California with many attributes of *Chlorostoma* (ventricose whorls, black-brown outer shell layer, absence of beaded spiral cords), recasts discussions of teguline phylogeny (Squires and Saul, 2005). A flat-sided, spirally beaded Cretaceous teguline, the late Maastrichtian *T. ovallei* Philippi, 1887, from central Chile (Bandel and Stinnesbeck, 2000), further demonstrates the pre-Miocene diversity and geographic distribution of tegulines.

As a consequence of these Cretaceous discoveries, an evolutionary scenario rejected by Hickman and McLean (1990), which placed the plesiomorphic *Tegula* near the base of the trochid group, gains credence, whereas scenarios inspired by the molecular data of Hellberg (1998) that presumed a strictly late Neogene timeline for teguline phylogeny are undermined by these Cretaceous data, as well as by early, middle, and late Miocene occurrences of tegulines in Peru.

The following observations provide some further constraints on phylogenetic hypotheses related to Tegulinae.

Peruvian Chlorostomine Group

The Peruvian chlorostomine group is comprised of four modern species: *Chlorostoma atrum*, *C. ignotum*, *C. euryomphalum*, and *C. luctuosum*. Gradations of sculpture indicate the latter two species may be one; *C. luctuosum* would be the senior synonym. Adding *C. quipua* extends the record of Peruvian chlorostomines to 9 Ma (Muizon and DeVries, 1985). This late Miocene occurrence precludes Hellberg's (1998) molecularly based hypothesis that these chlorostomines appeared in western South America during the late Pliocene and constitute a sister group to a North Atlantic Pliocene group of *Agathistoma* species.

The flattened base, open umbilicus, and spiral threads of *Chlorostoma quipua* indicate that it is most closely related to the modern *C. luctuosum*. Some specimens of *C. quipua* from upper Pliocene beds above Playa Huacllaco also have broad spiral cords like those on some specimens of modern *C. atrum*. A single upper Pliocene Huacllaco specimen has strongly convex spiral cords like those on specimens of the modern Chilean *C. ignotum*. This morphological variation suggests the onset of a radiation of South American chlorostomines near the end of the Pliocene. The late Pliocene was also a time of species-level molluscan mass extinction throughout the Peruvian Faunal Province (DeVries, 2001).

The origin of chlorostomines in Peru and Chile is not known. Tegulines are found, rarely, in lower and middle Miocene beds of southern Peru (*T.* (s.l.) *masiasi*; Figures 74–78), but they do not resemble late Neogene Peruvian *Chlorostoma*. Of Chilean Miocene species assigned to *Chlorostoma* (Nielsen et al., 2004), none exhibit the purple-black outer shell layer that characterizes the type species of *Chlorostoma* and most modern Peruvian chlorostomines. At three mm in length, *Tegula austropacifica* Nielsen, Frassinetti, and Bandel, 2004, is extraordinarily small for a chlorostomine. *Tegula chilena* Nielsen, Frassinetti, and Bandel, 2004, lacks the flattened base of chlorostomine species. *Tegula matanzensis* Nielsen, Frassinetti, and Bandel, 2004, resembles Californian specimens of *C. funebralis*, as the authors note, but the specimen lacks critical portions of the columella from which a better comparison can be made.

Chlorostomines appeared in southern Peru at the same time as the turbinid genus, *Prisogaster* Mörch, 1850 (DeVries, 2006), and mollusks with Panamic affinities (DeVries, 2006), an immigration pattern consistent with either a western North American or boreal Asian origin for the group. Molecular data (Hellberg, 1998) indicate Peruvian chlorostomines are more similar to Californian than Asian taxa. Shell characters are equivocal on this point. Protractive stripes, present on specimens of the oldest Peruvian chlorostomine, *C. quipua*, are also seen on some specimens of Californian *C. gallina*, *C. rugosum*, and Asian *C. nigerrimum* and *C. rusticum*. Protractive ribs, which occur in rare examples of *C. quipua*, are found on some specimens of the Californian "*Tegula*" *brunnea* and several Asian species. Imbricate subsutural spiral cords, which occur rarely on juvenile whorls on specimens of *C. atrum*, are most characteristic of the Californian *C. funebralis* (Figures 5, 6), are weakly developed on specimens of the Californian *C. gallina* and *C. rugosum*, and are not seen on specimens of Asian species.

Peruvian chlorostomines are distinguished from all Californian chlorostomines and all Asian taxa except a few specimens of *C. rusticum* by possessing a very thin and expansive umbilical veneer that does not bury the spiral umbilical cord. A thicker umbilical veneer drapes across the spiral umbilical cords in Californian and Asian specimens, largely burying the spiral umbilical cord and leaving visible only a blunt adaxial columellar tooth, a tooth at the base of the columella, and an intervening depressed nacreous wedge (e.g., *Chlorostoma funebralis*; Fig. 6). Peruvian chlorostomines also lack a second well developed tooth at the base of the columella, a character usually seen on Californian and Asian chlorostomine specimens (Fig. 6). These two derived characters–thin umbilical veneer, obsolete basal columellar tooth–may indicate that Peruvian chlorostomines are a sister group to Californian+Asian chlorostomines, with a common ancestor in the North Pacific Ocean older than late Miocene.

Cantallocostoma Group

Cantallocostoma is an endemic western South American genus characterized by beaded spiral cords and two

adaxially situated spiral umbilical cords. *Cantallocostoma panistostum* appears first in upper Miocene beds of southern Peru with other Panamic species (DeVries, 2002). It and the extant *C. quadricostatum* are unlike any Neogene or Recent teguline from Peru or Chile. Specimens of *Cantallocostoma* share with specimens of *Intistoma* the presence of two adaxially situated spiral umbilical cords (mostly covered by a thick umbilical veneer in specimens of *Intistoma*) and an erect columella with little in the way of a parietal flange or callus. Genetic data of Hellberg (1998), however, show no close affinity between *C. quadricostatum* and *I. aureotinctum*.

Intistoma Group

Intistoma has been created to include two very similar species, the modern Californian *I. aureotinctum* and early Pliocene Peruvian *I. pirqua*. Their distinctive spiral sculpture (strong bicarinate periphery, protractive subsutural nodes, three broad basal spiral cords), absence of a purple-black outer shell layer, absence of apertural teeth, and the isolation of *T. aureotinctum* in mtDNA phylogenies (Hellberg, 1998) indicate that neither *Chlorostoma* nor *Agathistoma* properly encompass these taxa.

Two other groups, one consisting of the modern northern Peruvian / Panamic *Tegula* (s.l.) *melalencos* and possibly *T.* (s.l.) *rubroflammulata*, the other comprising Miocene and Pliocene species from California [e.g., *T.* (s.l.) *dalli*], exhibit the distinctive subsutural spiral row of protractive nodes of *Intistoma*, but both lack the three broad basal spiral cords that characterize the new genus. The Californian Neogene species also lack the differentiation of spiral sculpture (coarse primary spiral cords, fine tertiary spiral threads overrunning primary spiral cords and interspaces) that is visible on well-preserved specimens of *I. aureotinctum*.

Tegula (s.l.) *tridentata* (Potiez and Michaud, 1838)

Tegula (s.l.) *tridentata* is a small teguline with a record in Peru and Chile extending no farther back than the middle Pleistocene. The distinctive purple-black exterior is shared with Peruvian chlorostomines, but the arrangement and number of columellar teeth is like that of Panamic species of *Agathistoma*. Mitochondrial DNA data (Hellberg, 1998) are not helpful on this point of phylogeny, as *T.* (s.l.) *tridentata* usually clusters with *Cantallocostoma quadricostatum*, which it resembles in only one significant shell character: two adaxial umbilical spiral cords, both terminating in a columellar tooth. For now, the proper phylogenetic assignment of *T.* (s.l.) *tridentata* remains elusive.

Austral *Agathistoma*

Panamic agathistomines, which are so speciose in warm waters of the Panamic Faunal Province, have been notably unsuccessful in penetrating the cold waters of the Peruvian Faunal Province. The only fossil agathostomine from western South America is a specimen from upper Pliocene beds of southern Peru assigned to *Agathistoma patagonicum*. A Miocene agathistomine reported from central Chile, *Agathistoma antiquum* Nielsen, Frassinetti, and Bandel, 2004, a Miocene occurrence of *A. patagonicum* reported from Argentina (Ihering, 1907; del Río, 1998), and an extensive record of modern *Agathistoma patagonicum* from southern Brazil to southern Argentina, including the Magellanic waters of Argentina (Carcelles and Williamson, 1951), if the synonymy of *A. fuscescens* and *A. orbignyana* with *A. patagonicum* is accepted (Forcelli, 2000), may point to a Miocene austral origin for the subgenus (Nielsen et al., 2004), rather than the Pliocene western Atlantic origin suggested by Hickman and McLean (1990). Alternatively, the monophyly of *Agathistoma* might be suspect; compact, beaded, multi-toothed austral tegulines with or without open umbilici might constitute a long-lived sister group to a group of Caribbean and Central American species.

CONCLUSIONS

Pre-late Miocene tegulines in southern Peru are exceedingly rare, poorly preserved, and bear little resemblance to late Neogene or extant taxa. During the early late Miocene, at least two lineages of tegulines, *Chlorostoma* and *Cantallocostoma*, entered Peruvian waters. It is unclear whether these two genera originated in California or Asia. Other trochids, namely *Diloma* Philippi, 1845, are thought to have dispersed across the Equator and across the Pacific Ocean from Australia, rafted by buoyant fragments of the brown kelp, *Durvillaea* Bory de Saint-Vincent, 1826 (Donald et al., 2005). Species of Peruvian *Tegula* likewise live upon on brown kelp (*Lessonia* Bory de Saint-Vincent, 1825) (Véliz and Vasquez, 2000; V. Mogollon, pers. comm., 2006), and thus may have been rafted to western South America from California or Asia in the same manner as *Diloma*.

Species of *Chlorostoma* and *Cantallocostoma* remained relatively unchanged until the end of the Pliocene, when a mass extinction swept away 80 percent of molluscan species in the Peruvian Faunal Province (DeVries, 2001). At that time, chlorostomines experienced a mini-radiation in southern Peru or Chile, with one species, *C. atrum*, eventually spreading to southern Argentina (Carcelles and Williamson, 1951). *Cantallocostoma panistostum* was replaced at the same time by the modern *C. quadricostatum*.

Another lineage of tegulines, represented by the early Pliocene *Intistoma pirqua*, appeared on Peruvian shores by the early Pliocene. Although the genus is now extinct in Peru, it persists in California in the guise of *I. aureotinctum*. It is likely that these species, with their broad basal spiral cords, are not related to the "*dall*" lineage of Californian tegulines that ranged from the early Miocene to Pliocene (Addicott, 1970).

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APPENDIX

Locality-samples. GPS = latitude and longitude coordinates obtained by a hand-held GPS unit. GE = coordinates obtained from satellite images available on-line from Google Earth™.

DV 211-3	Punta Lobitos, northern Peru, western point, terrace surface midway between sea cliff and inshore edge of deposit. 04°27′12″S, 81°17′25″W (GE; Lobitos 1:100,000 quadrangle). Upper Pleistocene.
DV 341-1	Quebrada Mogollon, northern Peru. Upper coquina of Mancora Tablazo. Lower Pleistocene.
DV 381-5	San Juan-Lomas road, km 47.5. Uppermost coquina. 15°22′59″S, 75°03′11″W (San Juan 1:100,000 quadrangle). Middle Pleistocene.
DV 382-1	San Juan / Lomas road, kilometer marker 50, flat-topped knoll south of highway. 15°22′02″S, 75°05′26″W (San Juan 1:100,000 quadrangle). Remnant of marine terrace. Upper Pleistocene.
DV 398-1	Playa Canastones, Bahia de la Independencia, Peru (Punta Grande 1:100,000 quadrangle). Recent.
DV 401-1	Hueco La Zorra, north end of beach. 14°02′31″S, 76°15′51″W (Punta Grande 1:100,000 quadrangle). Recent.
DV 463-1	Lower terrace, five km north of Chala (Chala 1:100,000 quadrangle). Upper Pleistocene.
DV 470-1	Above rocky road from Hacienda Tunca to Quebrada Huaricangana; hillside of brown sandstone. 14°56′ S, 75°09′ W (GE; Palpa 1:100,000 quadrangle). Lower Pliocene.
DV 478-2	Lomas Chilcatay, northeast end of outcrop. 14°11′42″S 76°06′57″W (Punta Grande 1:100,000 quadrangle). Chilcatay Formation, lower Miocene.
DV 571-1	Alto Grande, about one km south of intersection with abandoned paved road to San Juan de Marcona, on south-facing hillside west of Panamerican Highway; one of several shell banks. 15°26′57″S, 74°52′06″W (Acarí 1:100,000 quadrangle). Middle upper Miocene.
DV 809-1	Yauca, roadcut on western side of Panamerican Highway as it descends to valley floor. 15°39′49″S, 74°31′50″W (Yauca 1:100,000 quadrangle). Pisco formation. Lower Pliocene.
DV 1019-1	Gramonal, about one-half km east of canyon mouth. 14°45′50″S, 75°30′22″W (Lomitas 1:100,000 quadrangle). Middle Miocene.
DV 1029-1	Yauca Depression, west of Pana merican Highway. 15°39′29″S, 75°35′08″W (GPS, Yauca 1:100,000 quadrangle). Lower Pliocene.
DV 1032-2	Morro Abra de los Chaparrinos, descending from highest terrace level, north and south of second curve in Panamerican Highway. 15°52′59″S, 74°10′05″W (Chala 1:100,000 quadrangle). Upper Pliocene.
DV 1252-1	Quebrada de la Vaca, roadcut along Panamerican Highway, south of south wall, uppermost terrace above non-marine deposits. 15°48′56″S, 74°18′50″W (GPS; Chala 1:100,000 quadrangle).
DV 1254-Bal 6	Section along Panamerican Highway, ten km southeast of Chala and above Playa Huacllaco. 35 meters above basement rocks in measured section. 15°53′25″S, 74°09′52″W (GPS; Chala 1:100,000 quadrangle). Upper lower Pliocene.
DV 1254-Bal 10	Section along Panamerican Highway, ten km southeast of Chala and above Playa Huacllaco. 47.5 meters above basement rocks in measured section. 15°53′25″S, 74°09′52″W (GPS; Chala 1:100,000 quadrangle). Upper Pliocene.
DV 1284-1	Sacaco, shell banks southwest of north-south road to farmhouse (chacra). 15°33′03 S′, 74°43′50″W (GE; Yauca 1:100,000 quadrangle). Lower Pliocene.
DV 1355-1	Quebrada Pongo, one km upstream from juncture with Quebrada Caracoles. 15°30′22″S, 74°45′40″W (GPS; Yauca 1:100,000 quadrangle). Upper Pliocene.
DV 1372-1	Rocky beach on northwestern side of Punta Lomas (Acarí 1:100,000 quadrangle). Recent.
DV 1418-1	East side of Acarí Depression. 15°34′50″S, 74°36′59″W (GPS; Yauca 1:100,000 quadrangle). Upper Pliocene.

DV 1598-1	Roadcut along Panamerican Highway, descent from north into Yauca. Shell beds. 15°39′49″S, 74°31′50″W (GPS; Yauca 1:100,000 quadrangle). Lower Pliocene.
DV 1599-1	Hueco La Zorra, north end of beach (see DV 401-1). Recent.
DV 1635-1	Yauca Depression, west of Panamerican Highway. 15°39′33″S, 75°34′54″W (GPS; Yauca 1:100,000 quadrangle). Lower Pliocene.
DV 1648-1	Westward-facing side of valley, southwest of Cerros Colorado. 14°22′25″S, 75°53′52″W (GPS; Punta Grande 1:100,000 quadrangle).
DV 1713-1	Marine terrace on east side of Panamerican Highway north of road to Acarí. 15°36′09″S, 74°41′08″W (GPS; Yauca 1:100,000 quadrangle). Lower Pleistocene.
JM 82-19	Cerro El Huevo, northeast of San Juan de Marcona. 15°18′ S, 75°09′ W (San Juan 1:100,000 quadrangle). Upper Pleistocene.
JM 82-20	Cerro El Huevo, northeast of San Juan de Marcona. 15°18′ S, 75°09′ W (San Juan 1:100,000 quadrangle). Upper Pleistocene.
WJZ 345	Coquimbo, Chile. Pleistocene. Approximately 29°58′ S, 71°20′ W (GE).
Isla Ipun	Isla Ipun, Chile, shores of eastern embayments. 44°38′ S, 74°44′ W (GE). Recent.
Paracas Hotel	Beach south of Hotel Paracas, facing Bahía Paracas, southern Peru. 13°50′09″S, 76°15′ 19″W (GE, Pisco 1:100,000 quadrangle).